

Fig. 10. Ovum at a later stage (from ovary).

Fig. 11. Segmented ovum (from oviduct).

Fig. 12. Posterior extremity of embryo.

Figs. 13, 14, 15, 16. Head of embryo in different stages of development (seen from below): *a*, oral papillæ; *b*, antennæ; *c*, alimentary canal; *d*, opening of gullet; *e*, lateral growth of mouth; *f*, teeth-papillæ; *g*, superior growth of mouth.

XXXV.—*On the Fecundation of the Egg in the Common Fowl.*
By P. TASCHER*.

IN his justly celebrated work, '*Histoire générale et particulière du développement des corps organisés*,' M. Coste maintains that the egg of the hen is fecundated in the ovary long before being detached from this organ, and that a number of eggs are fecundated at one and the same time.

The latter of these assertions has been subjected to searching criticism by subsequent authors, and shown to be untenable; but the question as to where the fecundation of the egg takes place must still be considered an open one. Coste founds his conclusion partly on the microscopical appearance of not a few eggs in the ovary itself, indicating an incipient degeneration (a circumstance which does not, however, seem to prove the point, inasmuch as the process in question need not be caused by non-fertilization), and partly on certain experiments with hens which, after having been kept isolated, were paired 42 hours before an egg could be expected to be laid, assuming that exactly 48 hours elapse between the laying of each egg in the regular course. According to M. Coste, the egg requires 30 hours to pass from the ovary through the whole length of the oviduct; and his hens would consequently have been paired just 12 hours before the next egg was detached from the ovary; but in 12 hours the semen would, in his opinion, reach the ovary. In order to control this reasoning it is clearly necessary to verify carefully the time intervening between two subsequent eggs and the time occupied by the semen ascending the oviduct. For this purpose I have carried on continuous observations with a considerable number of hens, noting the exact time when each egg was laid; and I have come to the conclusion that the interval between the eggs is more correctly 44–46 hours in the case of hens laying every second day, and 26 hours in the case of those which lay every

* Abstract, sanctioned by the author, of an article in the '*Naturhistorisk Tidsskrift*,' Copenhagen, ser. 3, vol. x. 1875. This paper has obtained a prize from the Royal Danish Society of Sciences.

day, apart from the days of rest, representing intervals of 40–44 hours, which intervene with a certain regularity. With regard to the second point my results are equally at variance with those of M. Coste. The examination of more than 20 fresh ovaries, undertaken at times when semen ought to be found there if it ordinarily reaches the ovary, gave in most cases a negative result; only in two cases was living semen found; in three others some dead spermatozoa were observed. Only once was a living spermatozoon found outside a mature follicle, which was free from the infundibulum; of four follicles which were embraced by the infundibulum, three showed a few spermatozoa. I have never found spermatozoa inside an entire follicle. I therefore do not believe that the semen ascends to the ovary otherwise than quite exceptionally. In order to ascertain the time occupied by the semen in ascending through the oviduct to the infundibulum, several hens which had been kept by themselves for some time were paired, again isolated, and killed from 10–24 hours after. In one case, after 10 hours, a great quantity of living semen was found in the base of the infundibulum, but very little either in the other part of the duct or on the margin of the infundibulum; in a second instance the semen was found, 12 hours after pairing, in the upper part of the tube, but next to nothing in the infundibulum; in a third case, after 14 hours, much semen was found in the upper part of the tube and a little in the base of the infundibulum; in a fourth hen, after the same interval, the semen was found all over the infundibulum; in a fifth instance, after 15 hours, nearly all the semen had passed into the base of the infundibulum, but some remained in the upper part of the tube; in a sixth case, after 16 hours, semen was found all over the infundibulum, though but little occurred near the base; none was found in the tube; finally, in a hen which had been kept isolated for 24 hours after pairing, semen was found only along the margin of the infundibulum, in and above the “pitted zone” to be described hereafter. This hen had laid a sterile egg 23 hours after being paired, which consequently must have encountered the ascending semen a few hours before entering into the fourth division of the oviduct, in which the shell is formed. It cannot be doubted that some few spermatozoa remain in the duct; but it seems unquestionable that the semen ascends in bulk into the infundibulum; and my experiments show that it requires from 10–16 hours in order to reach the infundibulum, and at least 14 hours to reach the pitted zone.

I have no hesitation in saying that if M. Coste had based his experiments and arguments on the assumption of an in-

terval of 44–46 hours between each succeeding egg, and of 14 hours as the time required for the semen to traverse the length of the oviduct, he would not have concluded from this set of experiments that the egg is fecundated in the ovary.

The most probable conclusion from the facts as above stated is that the fecundation takes place in the infundibulum; and this appears to me to gain considerable strength from the circumstance that this part of the oviduct presents a very remarkable arrangement hitherto overlooked, the pitted zone already mentioned, which seems specially well adapted for retaining and preserving the semen.

The oviduct consists of four divisions, distinguishable by their physiological functions, viz.:—one, from its shape, is aptly termed the infundibulum, in which the egg is received from the ovary; a second, in which the albumen is secreted; a third, in which the shell-membrane is formed; and a fourth, producing the shell,—which last three represent the tubiform part of the duct.

But, however different the functions of these divisions are, their boundaries are by no means easily determined anatomically; each of them merges into the following one by gradual transitions. The folds of the infundibulum are simply continuations of those of the tubiform portion; and these are gradually transformed into the lower and at last shorter folds which are characteristic of the third and fourth divisions.

It is true that in some hens a kind of circular boundary-line, caused by the less-pronounced development of the folds in this line, may be observed between the second and third portion of the oviduct; but this is by no means clearly observable in all laying hens. The same may be said of two slanting transverse folds, which generally are seen near the base of the infundibulum, and which are caused by the greater thickness of the tube in proportion to the infundibulum; these folds appear less prominent in proportion as the infundibulum is more or less swelling and as its folds are thicker; sometimes they are entirely absent. The inside of the tube is wholly covered by a mucous epithelium forming numerous folds, which are supported in their interior by corresponding expansions of fibrous tissue. In the laying hen the epithelium is strongly ciliated and the folds highly turgescient. One might be tempted to say that the whole tube by its structure is adapted for retaining and even for preserving the semen. But I have not found the semen here otherwise than in passing, nor have I found any thing here that in any way appeared *specially* constructed to serve for the preservation of the semen for a longer time. With regard to the structure of the mucous

membrane of the tube and the infundibulum, I have, like many others, obtained microscopic images which in the most deceptive way simulated small sinuated or even contorted bag-shaped glands; but, by carefully comparing numbers of successive sections, I have convinced myself that there is not one single gland on the inner surface of the oviduct of the hen. I can entirely confirm the results of Grünwald in this respect (in the Handbook of Stricker, pp. 1189, 1190) as against the statements of Nasse, Meckel v. Helmsbach, Lereboullet, and Leuckart.

It is in the infundibulum that we must look for any arrangement that could serve as a receptaculum seminis; and I believe that I have discovered it there. The appearance of the infundibulum is extremely changeable. The general striking difference in the appearance of the oviduct in laying hens and in such as have not yet commenced laying, has often been pointed out. But besides this there is a great difference in this respect between hens still laying and such as are sitting or in a period of rest; and, finally, considerable individual differences may be observed between hens at the same stage.

When the young hen has moulted for the first time, or rather before the first moulting is accomplished, the oviduct increases enormously in size, the infundibulum is considerably expanded, new fusiform cells appear, older muscular fibres are extended, and the muscular layers increase in size. At the same time the cellular tissue swells considerably, becomes fibrous and covered by a ciliated epithelium. The following observations on the minute structure of the infundibulum of the laying hen are the results of the examination of more than twenty specimens:—The infundibulum is on the outside covered by the same highly vascular adventitious membrane as the tube. Inside the adventitia a fine fibrous tissue is found, in which more or less concentric bundles of indistinctly separated smooth muscular fibres are imbedded, running parallel to the margin. These bundles may be considered as constituting a direct continuation of the circular muscular stratum of the tube, just as upon the whole the infundibulum may be considered as an expanded continuation of the substance of the tube. Longitudinal muscles properly speaking are entirely absent, at any rate towards the margin of the infundibulum. There are many *apparently* longitudinal muscular fibres and bundles of such; but these appearances are caused partly by the vessels, partly by the frequent divisions and subsequent reunions of the transverse bundles, partly by the circumstance that the circular bundles near the anterior and posterior pointed extremities of the infundibulum are

drawn out into a point by the contractions of the mesometry. All these various muscular fibres form an areolar tissue of more or less close meshes towards the margin of the infundibulum, in the place where fimbriae begin to appear, and where, consequently, the infundibulum begins to increase in superficial area in an increased ratio. This areolar muscular tissue is supported by a corresponding stronger development of the cellular tissue; and in the part which, from the causes just mentioned, is increased in thickness, the large blood-vessels assume towards the margin a more parallel course, emitting or receiving the numerous branches which form the capillary tissue in the fimbriae. Towards the ostium abdominale the ciliated epithelium of the cellular or fibrous tissue often consists of several layers, and the tissue itself forms more or less sinuate and ramifying longitudinal folds, which decrease in height but increase in number towards the margin. The ciliated epithelium is often continued for some distance on the outside of the infundibulum, reaching in some cases to the ovary itself, the epithelium of which is not ciliated; in both places the epithelium is equally thin.

When the hen begins to lay, the oviduct has assumed a volume four or five times as large as in the full-grown chicken; the turgescence of the infundibulum is considerably increased, and the folds have become much larger, particularly in the foremost part of the infundibulum, which continues itself as a shorter or longer groove along the mesometry towards the ovary. The fibrous tissue continually grows more and more luxuriantly, so that the folds become broader and higher, at the same time emitting numerous lateral sinuated branches, which are often so numerous as to form dendritic figures*. The areolar muscular strata and vessels below the fibrous tissue swell correspondingly. The muscular bundles bifurcate and reunite, as is seen particularly in a zone running parallel to the crenulate more or less lobate margin of the infundibulum, at a distance from this of 1-3 millims. In this zone there is a broader muscular band along which the blood-vessels mostly run, which receive and emit the capillaries of the margin at angles approaching more or less to 90°. Outside this band a very pretty retiform arrangement may be observed in every laying hen—the muscular strata of the vessels forming anastomoses which, owing to the turgescence of the fibrous tissue, form regular meshes with

* I am aware that Grünwald denies the existence of these, even in the tube; but this result must be caused by the fact that, as he states himself, of the four specimens examined by him, three were only adult chickens which had never yet laid eggs.

depressed areas or pits lined with a strongly ciliated epithelium. In the middle portion of the margin of the infundibulum (the part nearest in front of the aperture of the tube) these meshes are smaller and more regular; towards the anterior part of the infundibulum they become longer, more irregular, and partly hidden by the folds which are here more strongly developed. The same formations are met with on the muscular band above mentioned and along its inner margin, under certain circumstances even in a peculiarly high degree of development. A series of considerably larger pits are met with on the right lobe of the infundibulum, reaching from its foremost free lateral lobe to the ostium infundibuli, decreasing in size hindwards. By degrees, as the muscles and folds swell, the pits become deeper and their margins increase in tension so much that they almost meet, and the meshes are converted into bags with small openings. Frequently muscles, vessels, and folds swell contemporaneously around a whole set of such bags, which thus will appear on the bottom of one larger pit, and this ultimately in its turn will be converted into a bag comprising the others. This latter arrangement occurs so frequently that it cannot be considered exceptional; but the small bags occur in every laying hen after the commencement of spring. In these pits and bags the semen finds protection; and most probably they contribute to preserve it. In this pitted zone along the margin of the infundibulum the semen is found spread, but, owing to the large superficial area, not closely packed. The largest number of spermatozoa I have found in a single bag is eleven. I have not found them alive later than the twelfth day after pairing.

After a time these bags degenerate; and this process first affects those situated in the middle part of the infundibulum, where, as already stated, they are smaller in size and more numerous. Gradually the bags increase in size; the ciliated cells fall off, leaving a thin transparent basal membrane, which now forms the wall of the bag; the little opening is closed. At first sight these appearances might suggest a hydropic state; but more extended examination proves that we have a normal state of degeneration before us. In the bags a very few spermatozoa may be found, generally sticking to the wall, sometimes several in small knots together. But the bulk of the contents is formed by degenerate ciliated cells, probably several generations, not only from the wall of the bag itself, but from the general surface of the infundibulum. By examination in a warm chamber (as proposed by Professor Panum) whole streams of loose ciliated cells may be seen,

however carefully one operates, passing along the folds. I have had no opportunity of instituting a comparison between these formations and the ovula Nabothi in mammalia; but their history exhibits a striking parallelism in some respects, in spite of the fundamental difference as to the place.

In the middle of the summer the tissues of the infundibulum continue to swell, so that the arrangement which, as it is seen in the spring, may be described as areolar, is now more properly described as spongy or cavernous; parts which formerly might be examined by an immersion-lens, now defy the application of any but low powers of the microscope. The right-hand lobe of the infundibulum swells so much along the zone above described, that particularly the anterior part becomes arched inwards; whilst the fimbriæ in this part for the same reason bend towards the outer side, where by degrees they fall off and degenerate, whilst a newly-formed margin, to take the place of the incurved portion, is already formed, mostly on the external border of the zone in question; sometimes even two new lobes may be seen almost parallel to each other. This circumstance explains why in such hens the bags are most frequently found in the extreme margin of the infundibulum.

When a hen has been laying for some time, she becomes exhausted, she ceases to lay, wants to sit, and a peculiar state of dissolution may be observed in all parts of the oviduct. The ciliated epithelium falls off, and the most distended portions of folds and margin also are loosened. In the general cavity of the body a considerable quantity (I found once as much as an ounce) of a yellowish brown liquid is collected, containing some small aciform particles and a great mass of ciliated epithelium from the oviduct. The whole of the latter, together with the mesometry, seem half-dissolved, and are very fragile. This state of things begins to show even before the laying is quite finished. In one case I found the cavity of the body full of the liquid, and the infundibulum quite ragged, in a hen which still had an egg in the lowest part of the oviduct, the largest follicle having a diameter of about 10 millims. If the hen is not allowed to sit, she begins to lay again after an interval of from six to twelve days, rarely more. This interval consequently suffices for the regeneration of the ciliated epithelium, as well as of muscular elements, in the oviduct and the mesometries. Towards the autumn, when the activity of the hen approaches its conclusion for the year, the volume of the oviduct and the infundibulum are considerably reduced during the period of rest, even if the activity is

resumed to a smaller extent. When the hen sits, the oviduct is much reduced and loses its ciliated epithelium.

I have stated that the right-hand lobe of the infundibulum was generally more abundantly supplied with pits and bags than the left; and a similar difference is observed also with regard to the turgescence and luxuriant growth of the parts generally. The portion most affected is the anterior part of the right lobe, near the pointed part which stretches along the anterior mesometry towards the ovary. Here the right lobe always develops a more or less expanded, almost rectangular secondary lobe; at the same time, in the highly turgescient state, the pitted zone is arched inwards against the anterior narrower part of the infundibulum. Thus a kind of indentation is formed between the turgescient lobe and the narrow anterior part of the infundibulum. This indentation corresponds in size to the stems of the folliculi, and catches round them, collar-like, when the infundibulum has seized the follicle. The expanded right lobe then closes round the follicle in the shape of a cupola and pulls against the contractions of the mesometry, by which the ripe follicle and in part the ovary are drawn backward—a process which no doubt contributes to the bursting of the follicle. Only one case has occurred to me in which the left side of the infundibulum was more developed than the right.

I believe myself justified in concluding that this pitted zone serves to arrest the progress of the semen and to preserve it—in short, that it constitutes a true receptaculum seminis—and that the fecundation of the eggs takes place in the infundibulum, on the egg coming into contact with the semen by the bursting of the follicle. Not having met with living semen in the pitted zone later than the twelfth day after the pairing of the hen, I assume that it does not generally keep longer; and it is in good keeping with this view that fertile eggs, according to Coste's and my own experiences, are not often laid after the eleventh day, though instances have occurred of the last fertile egg being laid on the seventeenth or eighteenth day. But in these cases the hens have not been laying regularly; and though a successful pairing has been known to suffice for eight fertile eggs, its efficacy generally reaches only to five or at most seven, the subsequent eggs being sterile without renewed pairing of the hen.